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JOINT FORMATION AMONG THE INVERTEBRATA.

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The following observations were prompted by a discussion on the subject of joints, at a meeting of the Academy of Natural Sciences of Philadelphia held on November 22nd, 1892, when Prof. Cope considered some facts relating to his theory of joint formation as seen among the vertebrata.

As his theory has been known for some time, and an extended consideration of it has recently been published¹ I merely quote as a thesis, a sentence published in 1878²; "change of structure is seen to take place in accordance with the mechanical effect of three forms of motion, viz, by *friction*, *pressure* and *strain*."

It occurred to me that if his theory had a general application, some additional proofs could be shown to exist among the invertebrates, where we have the action of muscular force upon hard and resisting parts of the skeleton. Those which present the best study for this purpose, appear to be the crustaceans, where we find an immense variety of articulations in the body and in the limbs; highly complicated locked joints, others allowing motion in but one plane, as well as

¹The Mechanical Causes of the development of the Hard Parts of the Mammalia, by E. D. Cope. Jour. of Morph. Vol. III, 1889, p. 137-290.

²The relation of animal motion to animal evolution, by E. D. Cope, American Naturalist, Vol. XII. 1878, p. 44.

loose joints, where the hard parts scarcely come in contact with one another, and cases of degeneration of the hard parts, leading to total disappearance of a previously existing joint.

In the annelides, from which, there is no doubt, the arthropod branch sprang, we find no deposit of inorganic salts in the epidermis. (I do not regard the hard, calcareous, and other secretions of tubicolous annelides as entering into this question, as they are merely protective coverings, not acted upon by the muscles of the body, nor is there even any muscular connection with it.) The outer layer of the body is generally of a horn-like character, adhering closely to the secretive cells of the epidermis, very flexible and thrown into folds by the vermicular motion of its possessor. In the leeches, the body consists of a flexible cylinder, made up of two sets of muscles, an outer longitudinal cylinder and an inner cylinder of circular fibers, the contraction of which, causes the animal to increase in length, while shortening is effected by the contraction of the longitudinal layer. The external surface of the medicinal leech, for example (see fig. 1)

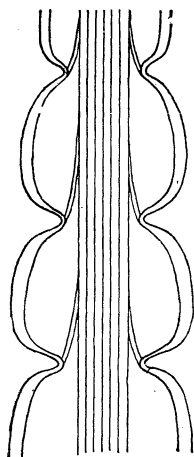


Fig. 1

Diagrammatic representation of the segments of the leech showing the folds, valleys and muscular fibers.

is thrown into a regular series of very fine folds, extending across the longitudinal axis of the body. These folds do not correspond in numbers, to the somites of the body, which are not indicated externally, five, six or more of them belonging to one somite. When the animal shortens its length, these folds are deepened and the segments thrown closely together; when extension takes place, the folds are flattened, spread open, although not wholly disappearing, as they are a fixed quantity so to speak. I believe these folds are due to mechanical action: by the disposition of the different fibers of the longitudinal series, in being inserted in a series of planes bounded by the

valleys between the folds, this being aided by some of the circular fibers which pass through the longitudinal sheath, and find their attachment to the bases of the valleys.

Starting from this point, and supposing the regularity of the folds to have become established from pre-existing irregular folds by the regularity and stress of muscular action, we can conceive that when deposits of calcareous matter took place, rings similarly formed by a folding of a soft skin would receive that deposit at the most prominent portion of this fold, the convex face and not in the protected valleys, as there would be more friction or pressure from external causes, and no deposits would take place in the valleys themselves because they would not be subject to external friction, and their continual flexion would prevent any such deposits. Should such a deposit take place in the valleys, there would be a stiffening of the whole surface which would defeat motion. In fact, in the leech, the cuticle is already much thicker on the crests of the folds than in the valleys.

In the more primitive crustacea, we find the animal made up of rings extending over the whole length of the body, similar to the rings of the leech, save (fig. 2) that there is but one ring

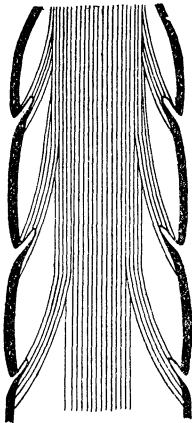


Fig. 2

Diagrammatic representation of the rings of a primitive crustacea showing the action of the muscles.

to one somite, and instead of a perpendicular valley between the folds, this valley has an inward and a forward direction, allowing the anterior edge of a caudad ring to fit into the posterior edge of a cephalad ring.

In the higher crustacea, several of the anterior rings have coalesced, and form a solid shield which is known as the carapace. This has no doubt arisen by the lessening of the action between the anterior rings when the posterior portion of the body became the more active propelling organ. As the action ceased forward the valleys came to rest, and became exposed to friction and pressure, and

consequently a deposit of calcareous matter took place producing the stiffening above hinted at.

The formation of jointed appendages from parapodic paddles of the annelides can be followed out in the same manner, since the manner of mutual relation of the segments is the same as in the case of the body segments.

It has been stated that in the leech the folds do not correspond in number to the somites of the body, while they do in the crustacea. All annelides do not move by means of a muscular system built upon the plan found in the leech. In many the circular layer has to a large extent disappeared, for the longitudinal-circular plan is undoubtedly ante-annelidan. The movement of the free medusoid forms, and of the Ctenophora, is the result of a modified arrangement of this plan.

With the disappearance of the circular layer, we find a peculiar modification of the longitudinal layer. This layer becomes broken up and the fibers act in moving the setæ, which answer to limbs. In a segment of a setiferous annelid, we may observe that the longitudinal muscles of the somite in section at the position of the seta are arranged like the letter "V," in the fork of which the seta lies, the fibers to the left (anterior) pull the seta externally backward, those on the right (posterior) pull the seta forward. The introduction of the setæ, the origin of which I do not here attempt to explain has no doubt been, together with the establishment of external segmentation, a strong factor in causing the breaking up of the muscular tube into sections (myotomes), which by use and consequent increase have extended each arm of the "V" into the segment on each side, while the insertion of the end of the seta has caused a break in the muscle by the formation of an aponurosis. This gives us the peculiar disposition of a myotome to extend arcross the union of two somites.

If we examine the segments of the so-called abdomen of the macrurous crustacea, as the lobster, we will find that the anterior face of one abdominal ring is pulled into the posterior orifice of the ring lying anterior to it, forming a kind of tubular ball and socket joint, but with a flexible part of the integument with no calcareous deposit, folded upon itself,

and acting physiologically as a tubular *ligamentum teres*. On examining the different joints, we will find that commencing at a fixed point, as at the base of the thorax, the movable ring of the first abdominal somite is *pulled into* the fixed part. Then the first abdominal somite becomes the fixed point for the movable ring posterior to it, and so on, so that we find that the rings proceed away from the thorax, each is pulled into the opening of the one in advance. This is true of all those forms where the abdomen is well formed, strong and an active organ in the economy of the animal; when this organ, the abdomen, ceases to be an active organ of motion as in the burrowing forms, as *Callianassa*, *Gebia*, some of the *Squillidæ*, etc., or where it is folded upon the sternum of the thoracic region, the muscles becoming weaker through disuse, the rings are not subject to the powerful muscular strain, and they as a rule overlap but little if at all, but lie so that the edge of one ring rests upon the edge of another. In those forms where degeneration of the abdomen has proceeded so far as not to have even the usual deposit of calcareous matter, as in the hermit crabs, there are simply indications of rings on the abdomen, and this organ is but little more than a fleshy sac containing some of the viscera, and supplied with a few muscles which act together, with the form of the organ, to keep the abdomen curled so that it may hold as a hook, the animal within the molluscan shell which it habitually occupies.

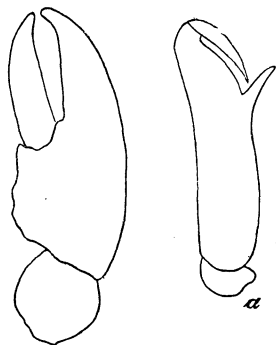
In forms as highly developed as the cray-fish and the lobster where the calcareous deposits are great, there have crept in many modifications. One of the main features in the articulations of the rings of the abdomen is the "lock" or hinge which allows no lateral movement in the tail whatever; the lateral movement is also prevented by the overlap of the pleura. This lock consists of a rounded prominence on each of the rings projecting *forward* from a posterior segment into a socket in the anterior one. The movement in any two segments so formed takes place in the plane, the axis of which passes through these two points so that the arc described by the movement is only in a vertical plane. The terga of the segment is much arched in the lobster, and the upward motion is limited after a certain point is reached by the dome

of the segment itself. In some of the *Scyllaridæ*, there is a transverse groove on the terga of the somites merely indicated in the lobster, into which the posterior face of the terga ahead of it fits when the abdomen is fully extended, and which prevents any further upward movement. It will be noticed further, in those forms that the sternum of each abdominal segment is very narrow, and that they are connected by a broad uncalcified membranous area which allows plenty of room for flexion downward.

The first abdominal segment is narrow, and in the vast majority of cases it is *considerably* narrower than the one which follows it so that it may be covered by the posterior edge of the carapace and the anterior edge of the second abdominal ring. In the *Homaridea* and *Loricata* there is an interesting provision to prevent the strain of the powerful abdominal muscles from drawing the smaller segment too far into the thorax. On each of the lateral faces of the ring there is a broad tooth or calcified lobe, which overlaps the posterior edge of the carapace allowing the latter to play between it and the surface of the ring.

When the limbs are examined, the same rule will be found to hold good viz.: that the movable part is pulled into the fixed part. A modification of this is well illustrated in the evolution of the large chelæ. In some forms, take for example *Ibacus*, the first pair, and in fact all of the thoracic limbs end in a sharp pointed segment, there being not the slightest suggestion of a chela. In *Crangon*, (fig. 3) on the other hand,

the terminal segment is pulled against the broad face of the penultimate one thus making a shift for a chela. In the Stomatopoda this step has been developed, for the last segment can be drawn against the whole length of the penultimate one (which is sometimes grooved to protect the points of the spines of the latter,) and forms with it a very effective grasping organ. The continual use of the terminal segment, the increase of the muscular power



b Fig. 3

- a*. "hand" of a form of *Crangon*.
b. "hand" of a form of *Astacus*.

will tend to draw this terminal segment backward (into) on the penultimate which enlarges with the increase of bulk of muscle, so that a well developed chelæ, as in the lobster, is found where the ultimate segment is pulled backward to about the middle of the penultimate segment.

A true ball and socket joint rarely if ever obtains in the crustacea, and for very obvious reasons. The nature of the impassive connection of the joints would not allow of the motion and the active element, the muscle acts upon the *inside* of the joint or through its center, thus making it almost impossible for muscles to act so as to give the free movement of a ball and socket joint. The same end is obtained by a series of ginglymoid joints working in different planes so that in a series of three or four joints the end of the limb, for example, can be made to describe a circle, and I am inclined to believe that in order to obtain this free motion, the first two or three joints of crustacean limbs are as a rule very short and work in different planes.

Several objections may be easily found to the statement that posterior segments are always drawn into the anterior ones. Take for example, the shrimps, where the *second* abdominal ring *overlaps* the first so that the ring ahead of it as well as the others behind it is drawn within its anterior opening. I am inclined to regard this exception as more or less proving the rule, and to consider the second segment the fixed point into which the other two rings are drawn. We see a foreshadowing of this plan in the lobster group, where, as in *Astacus*, to use the words of Huxley, "the pluræ of the second somite are much larger than any of the others, and their front edges overlap the small pleuræ of the first abdominal somite, and when the abdomen is much flexed these pluræ even ride over the posterior edges of the branchiostegites."³

An exception much more difficult to explain is that found in some of the anomurous forms as *Galathea*, where the fourth, fifth, sixth and seventh segments follow the rule, and the first

³The Crayfish, an introduction to the study of zoology, by T. H. Huxley, New York and London, 1880, p. 98 and 99.

in regard to its anterior face, but the second overlaps the first, the third, the second, and the fourth. In other words, the fourth has pulled both ways as the second has in the shrimps, but in the latter the second segment is obviously the largest of the series, while the abdominal segments of *Galathea* are all of about the same size and strength.

We may, however, provisionally accept as a natural consequence and general rule, that the motion of a movable part naturally hollows out for itself a cavity in which to move within the solid and fixed basis. This may be further illustrated in the hard parts of the vertebrata.

It is a well known fact that even when the muscles are said to be at rest, there is more or less of a strain, or pull exerted. When the human hand hangs loosely down, it rests half way between extreme flexion and extreme extension; the same may be said of the fingers, although in some persons, as in sailors, where the flexor muscles are very strong the fingers hang as so many "hooks," owing to the pull of the more powerful flexor muscles. This is well shown in cases of the paralysis of one set of muscles; the parts are drawn to the side of the healthy muscles even when no voluntary action is exerted by the normal muscles. This is too well known to medical men to require further comment, and is especially illustrated in cases of facial paralysis where the face is drawn strongly to one side by the normal muscles.

Taking the action of the normal muscles when at so-called rest, it is not surprising to find that in the joints the lighter or more mobile part, being continually pulled against the fixed part and moved upon it, that a cavity should be formed in the fixed parts by the continual action and pressure of the mobile part. Take for example, the humerus in man, the head is hemispherical and fits into a concave portion of the scapula, a true ball and socket joint, and it is formed, if there be any truth in the idea, by the humerus being pulled into the scapula by the powerful muscles of the shoulder. And as this is probably the first joint which was formed in the evolution of the limb which then acted as a fin, the rotatory motion aided and finally established the ball and socket form

of joint. Other cases might be mentioned as that of the lower jaw and the tarso-tibial joint.

In the above remarks, I have simply made an attempt to apply the theory of mechanical genesis to a much neglected group of the invertebrata, and if I, in this, have only been able to direct attention to the field of carcinology, I will feel that this short paper will have served its purpose.